

Ultrastructure and taxonomy of the Order Watznaueriales

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The Order Watznaueriales is a group of Early Jurassic to Recent placolith heterococcoliths that are united by a common ultrastructure. Either two or three shields are present, the lower two shields having R-unit elements, and the third shield, when present, having V-unit elements (Figure 1). An R-unit tube cycle is usually present, as well as a central-area structure that can include plates, axial crosses, transverse bars, or may be open. This ultrastructure is quite different from other placolith families, which usually have R-unit proximal shields and V-unit distal shields. Three families are placed within the Order Watznaueriales: Bussoniaceae, Ellipsagelosphaeraceae, and Noelaerhabdaceae. The Noelaerhabdaceae have generally been considered to have evolved from the Family Prinsiaceae (Order Isochrysidales). However, the ultrastructure of the Noelaerhabdaceae has much more in common with the Ellipsagelosphaeraceae.

The Watznaueriales appeared during the Early Jurassic with the evolution of the genus *Mazaganella* (Family Bussoniaceae) from the ancestral murolith genus *Crucirhabdus*. The key innovations in *Mazaganella* were a doubling of the R-unit proximal cycle and development of a lateral extension of both the proximal and distal cycles, resulting in a placolith morphology with two proximal shields and a raised distal shield. *Bussonius* then evolved from *Mazaganella* with the inception of imbrication in the shields. In a separate branch of the family, *Triscutum* evolved from *Mazaganella* through the development of a high non-imbricate distal shield.

The Family Ellipsagelosphaeraceae evolved with the appearance of *Lotharingius* in which the raised V-unit distal shield of *Bussonius* was reduced in height and width until it was close to level with the distal surface of the upper of the two proximal shields. This relict V-unit cycle is here referred to as the crown cycle. The upper of the two R-unit proximal shields in *Bussonius* became the distal shield in *Lotharingius*. The R-unit distal shield in *Lotharingius* and all subsequent descendants has no homology to the V-unit distal shield of the Bussoniaceae. The basic ultrastructure of *Lotharingius* continued through the Mesozoic with the appearance of *Ellipsagelosphaera*, *Watznaueria*, *Cyclagelosphaera*, and *Ansulasphaera*, all of which have a crown cycle and R-unit proximal and distal shields. Only *Cyclagelosphaera* survived the K/Pg boundary mass extinction, and it is still extant as *Tergestiella*.

In the Ypresian, *Cyclagelosphaera* gave rise to *Cyclicargolithus* in the Family Noelaerhabdaceae through the complete loss of the V-unit crown cycle. The Ellipsagelosphaeraceae and Noelaerhabdaceae have in common two R-unit shields, an ultrastructure not seen in any other placolith group, which is considered strong evidence of a very close relationship between the two families. The basic ultrastructure of *Cyclicargolithus* has been conserved from the Ypresian through Recent in *Reticulofenestra*, *Dictyococcites*, *Cribrocentrum*, *Crenalithus*, and *Pseudoemiliana*, and in the extant *Gephyrocapsa*.

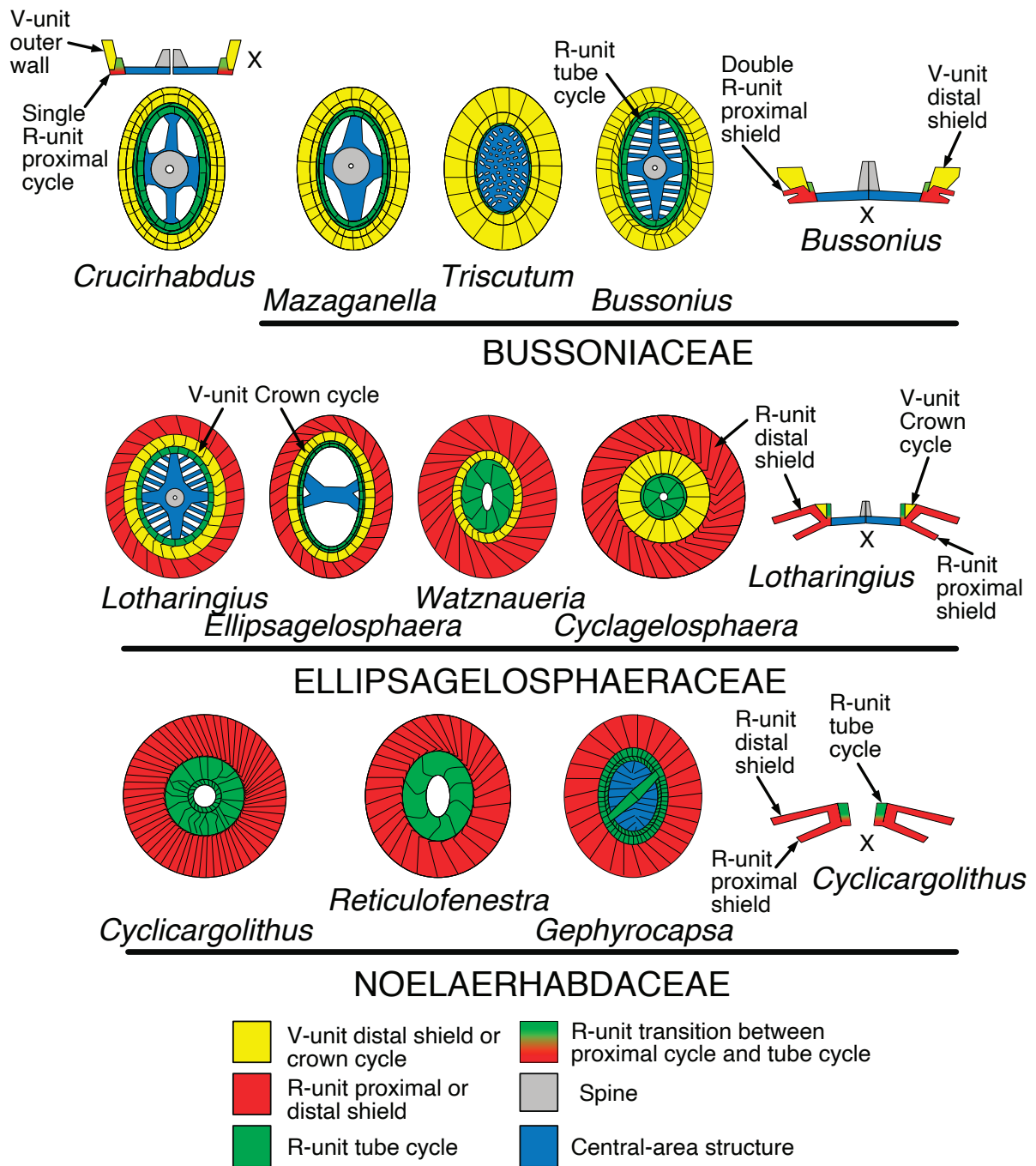


Figure 1. Schematic distal side ultrastructure of the Order Watznaueriales. X = cross section.